Predation upon *Crassostrea virginica* (Gmelin) Larvae by Two Invertebrate Species Common to Chesapeake Bay Oyster Bars [1]

BY

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INTRODUCTION

THORSON (1950, 1966) DISCUSSED the high mortality of marine planktotrophic larvae and the dominant role played by predators in this mortality. MILEIKOVSKY (1974) expanded on this topic, concluding that the ecological significance of such predation was still unclear with more reliable quantitative data necessary. KORRINGA (1941) found that predation was the major cause of mortality in larvae of the European oyster (*Ostrea edulis* Linnaeus, 1758). Mature larvae of the American oyster, *Crassostrea virginica* (Gmelin, 1791), tend to be concentrated on or near the bottom of estuaries during ebb tide and slack water periods (CARRIKER, 1967; WOOD & HARGIS, 1971). Further, settlement of pediveliger larvae of oysters has been shown to be gregarious in nature (HIDU, 1969; HIDU *et al.*, 1970), presumably resulting in aggregations of larvae over suitable substrate in response to a water-borne pheromone (VEITCH & HIDU, 1971). Such gregarious behavior should increase mortality rate of larvae due to predation by benthic organisms, especially those invertebrates inhabiting shell surfaces of oyster bars which are major areas of oyster larval settlement (CRISP, 1967). In order to begin to establish significance of predation by such benthic invertebrates in Chesapeake Bay, in the summer of 1977 we investigated 2 common species, namely a sea anemone, *Diadumene leucolena* (Verrill, 1866) and a barnacle, *Balanus improvisus* Darwin, 1854.

Diadumene leucolena is found on oyster beds throughout Chesapeake Bay, occasionally occupying 15-25% of the surface area of live oyster shells (CONES & HAVEN, 1969). Predation by sea anemones may be restricted mainly by their ability to seize and swallow prey, as annelids, mollusks and crustaceans can all be ingested (STEPHENSON, 1928). WILLIAMS (1972) found the main components of gut contents of *Diadumene luciae* (Verrill) to be amphipods, isopods and copepods. MACKENZIE (1977) recently reported preliminary observations that *D. leucolena* from Chesapeake Bay will feed on mature oyster larvae. We wished to quantify predation intensity, feeding rates and digestion times for this sea anemone.

SOUTHWARD (1955), BARNES (1959) and CRISP (1964) indicated that barnacles feed on a wide variety of planktonic organisms ranging in size from flagellates to small crustacea. Maturing oyster larvae may range in size up to 300 μm (GALTSOFF, 1964; CHANLEY & ANDREWS, 1971), placing them within the reported size range of ingested material. *Balanus improvisus* is very common in Chesapeake Bay (WASS, 1972) often settling thickly on oyster shell. It should have every opportunity to prey on oyster larvae as they occur over oyster beds. We wished to test the assumption that *B. improvisus* will ingest mature oyster larvae.

We report here the results of our study of predation on mature *Crassostrea virginica* larvae by these 2 common invertebrate inhabitants of Chesapeake Bay oyster bars.

MATERIALS AND METHODS

Adults of both species were collected by oyster dredge in the Choptank River, Maryland (approximately 38°40′N; 76°10′W) during the summer of 1977. Pieces of shell carrying *Diadumene leucolena* or *Balanus improvisus* were chipped off oysters. Only sea anemones which remained

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attached to a shell fragment were used in experiments. This was generally true for *B. improvisus* as well, although occasionally barnacles not attached to a shell fragment but retaining their calcareous basis were used. All animals were maintained in aerated Choptank River water in the laboratory with collection and experimental salinities ranging from 9 to 11‰ over the summer. Experimental water temperatures were kept at 21° to 22°C, a few degrees Celsius below collection temperatures.

Oyster larvae were obtained from our laboratory's shellfish hatchery. Pediveliger or "eyed" larvae were collected on a 177 μm mesh screen and the younger umbo larvae on an 88 μm mesh screen. Water in which larvae were held was first filtered through a 10 μm filter. Over long holding periods, oyster larvae were fed cultured algae. During our experiments larval numbers were estimated as follows: Immediately after the water in their containers was mixed thoroughly with a non-rotary movement, a 1 mL sample was taken and the larvae therein were counted in a Sedgewick-Rafter cell. This was repeated 10 times and a mean value was determined and used to extrapolate to the number of larvae in the volume of water being sampled. When different prey densities were needed, they were obtained by concentrating larvae in a volume of water to a known larval density and then pipetting appropriate quantities of this "stock solution" (after brisk agitation) to filtered water to provide for the experimental densities desired.

Observations were made on individuals of each of the invertebrate species to observe their behavior in the presence of oyster larvae. In all experiments, individuals used were not fed in the 24 h period from time of collection until feeding observations began. Each invertebrate was placed in the experimental containers (11 to 20 cm diameter glass bowls) at least 6 to 18 h before larvae were introduced. Observations were made using a dissecting microscope at a magnification of 15 to 20×. Experiments were made on each of the species as follows:

Diadumene leucolena

Ingestion of Larvae: Observations were made over 15 to 60 min on feeding behavior of individual sea anemones in the presence of umbo and pediveliger oyster larvae and details were noted. During experimentation, 3 arbitrary size classes of *Diadumene leucolena* were used, based on pedal diameter of the attached animal: small (2 - 4 mm), medium (5 - 8 mm) and large (9 - 11 mm).

Two experiments were performed to study larval ingestion using varied densities of predator and prey. The first experiment lasted 48 h and involved pediveliger densities of approximately 0.1, 0.4 and 1.6 larvae mL^{-1} and the presence of either 2 medium sea anemones or 1 small, 1 large and 3 medium sea anemones. Controls contained no sea anemones. The second experiment lasted 24 h with larval densities of approximately 1.6, 3.2 and 6.4 larvae mL^{-1} and predator densities of 1 or 2 medium sea anemones. At the end of each experiment, numbers of surviving larvae were determined by subsampling and in addition, the shell fragments and walls and floors of the containers were examined carefully for settled larvae (none were found).

Feeding Rates: Umbo or pediveliger larvae were added to 200 mL of water in 11 cm bowls containing single *Diadumene leucolena* which were then observed during feeding. Number of larvae ingested by sea anemones was counted over a 10 min period, beginning immediately after 1 larva was seen to be eaten. Ingestion was determined to occur when a larva travelled far enough down a sea anemone's pharynx to become lost from view. Size of sea anemone, larval density and larval stage were varied in these experiments.

Digestion Times: Sixteen individual sea anemones of varying sizes were allowed to ingest at least 10 pediveligers while under observation. They were then placed in water in clean bowls which were checked every 30 min for empty pediveliger shells. Time to appearance of shells was noted in each case.

Egestion and Gut Content Analysis: Forty-five sea anemones freshly dredged from the Choptank River were isolated on oyster-shell fragments, rinsed gently and then placed in individual clean glass bowls. Six to 12 h later, the shell fragments and bowls were examined for the presence of larval shells as evidence of predation on bivalve larvae in the field. In addition, gut contents of 1 laboratory-fed and 10 additional freshly dredged sea anemones were examined after dissection.

Balanus improvisus

Ingestion of Larvae: Two arbitrary size classes of barnacles were established based on greatest opercular diameter: small (2 - 4 mm) and large (5 - 8 mm). Known densities of umbo or pediveliger larvae were added to 11 cm bowls containing single barnacles which were beating their cirri. Control bowls contained no barnacles. After 18 h, the barnacles were removed, their shells and bowl surfaces were searched for settled oyster larvae and numbers of larvae surviving were determined by subsampling.

Egestion and Gut Content Analysis: Twenty-five freshly dredged barnacles were rinsed and placed in individual clean glass bowls which were examined 10 to 12 h later for shells of bivalve larvae. If feces were present, they were examined for larval shell fragments resulting from mastication by the barnacles (Nicol, 1967). If no feces were present, the barnacles' gut contents were examined after dissection. An additional 10 barnacles were allowed to sit and beat their cirri in a container containing pediveligers with a density of 20 larvae mL^{-1} and their feces or gut contents, or both, were examined at intervals over a 10 to 12 h period.

Field Population Samples: We wished to determine densities of *Diadumene leucolena* and *Balanus improvisus* on oyster bars in Maryland's portion of Chesapeake Bay to estimate the potential for predation in nature. Sixteen oyster bars were sampled using a towed oyster dredge. Of the dredged material collected from each oyster bar, 30 L were shoveled into a container and the contents of the container (live oysters, shell, shell fragments) were then processed immediately by close examination of all surfaces of the dredged material. Total numbers of *D. leucolena* were readily obtained. Because of high densities of small barnacles, no attempts were made to differentiate between *B. improvisus* and *B. eburneus* Gould, 1841, another barnacle found in some parts of the Bay that we sampled; our data are counts of barnacles in general.

RESULTS

Diadumene leucolena

Feeding Behavior: Introduction of oyster larvae elicited pre-feeding behavior in *Diadumene leucolena* similar to that described by McFarlane (1970) in *Tealia felina.* In *D. leucolena,* this behavior consisted of widening of the oral disc, raising and spreading of tentacles, and protrusion and opening of the actinopharynx. This pre-feeding response was quite stereotyped except for actinopharynx protrusion, which did not occur in some animals.

Feeding behavior in *Diadumene leucolena* was similar to that of *D. luciae* as described by Williams (1972), and his terminology is used here. The feeding response consists of 3 distinct actions: snatch, tentacular response, and oral response. The snatch occurs as a larva contacts and adheres to a tentacle which contracts quickly, although not completely. There is often a movement by the distal end of the tentacle to encircle the larva. A snatch response to a single larva never involved more than 2 tentacles. The tentacular response follows the snatch and consists of the tentacle bringing the larva to the oral disc, which begins to expand. The oral response occurs as the larva is transferred from the tentacle to the lips of the actinopharyngeal region, with the latter expanding outward toward the tentacle as the mouth opens. The larva is transported inside the anemone with the transport system almost certainly being the pharyngeal cilia, although these were too small to be seen.

An egestion response was observed in *Diadumene leucolena* that was similar to the oral response, with the direction of transport reversed. The mouth opened, although to a smaller extent than in feeding, and the egested larval shells were transported to the edge of the oral disc where they dropped to the substrate. Whenever more than 1 shell was egested at one time, the shells clung together in a clump.

Ingestion of Larvae: Table 1 contains results of the 2 ingestion experiments. Sea anemones fed heavily on pediveliger larvae as few larvae survived in the bowls with sea anemones whereas survival in control bowls was always much higher, usually by an order of magnitude. Decreased larval numbers in controls were presumably due to natural mortality and inevitable errors in sampling when adding larvae at the start of the experiments and counting survivors at the end. Variations in larval density and sea anemone size or numbers did not affect the results.

Feeding Rates: Results of feeding rate experiments are contained in Table 2. About 25% of the sea anemones initially used did not feed and were not considered when computing feeding rates. Rate variations were large, as would be expected for an individualistic process such as feeding. Rates were compared using Students' t-test after we had determined that variances were homogeneous as indicated by results of the Fmax-test (Sokal & Rohlf, 1969). Feeding rate increased as larval density increased, with the differences statistically significant for medium individuals feeding on umbo larvae ($P < 0.05$; experiments 3 and 4) and pediveligers $P < 0.01$; experiments 7 and 8). Medium-sized individuals generally fed at a higher average rate than did smaller sea anemones, except in the presence of low densities of umbo larvae (experiments 1 and 3); however, these rate differences with size were statistically significant only for sea anemones feeding on high densities of pediveligers ($P < 0.05$; experiments 6 and 8). Small sea anemones ate fewer umbos min^{-1} than pediveligers min^{-1} whereas medium sea anemones ate fewer umbos min^{-1} than pediveligers min^{-1}; these differences were not statistically significant ($P > 0.05$).

Table 1

Crassostrea virginica and *Diadumene leucolena.* Ingestion of pediveliger larvae under varying conditions of predator and prey density. Controls—no sea anemones. I. 48 h experiment. Water volume = 1.75 litres. Numbers of sea anemones per container: A—Two medium (5-8 mm pedal diameter); B—One small (2-4 mm), one large (9-11 mm) and three medium. II. 24 h experiment. Water volume = 0.25 litre. A—one medium sea anemone; B—Two medium sea anemones.

		Larval numbers			
		Replicate 1		Replicate 2	
Approximate pediveliger density	Anemone density	Start	Finish	Start	Finish
I. 0.1 ml^{-1}	A	174	20	—	—
	B	174	3	—	—
	Control	174	118	—	—
0.4 ml^{-1}	A	740	2	702	1
	B	740	4	702	1
	Control	740	697	702	102
1.6 ml^{-1}	A	2775	6	2808	69
	B	2775	6	2808	20
	Control	2775	2147	2808	1006
II. 1.6 ml^{-1}	A	400	13	400	3
	B	400	1	400	2
	Control	400	131	400	118
3.2 ml^{-1}	A	799	16	799	0
	B	799	77	799	7
	Control	799	665	799	432
6.4 ml^{-1}	A	1598	1	1598	38
	B	1598	2	1598	25
	Control	1598	826	1598	812

Table 2

Crassostrea virginica and *Diadumene leucolena.* Feeding rates of two sizes of sea anemone on two stages of oyster larvae. Single anemones in 200 ml of estuarine water were observed for 10 min after feeding began. N = number of replications. Feeding rate = average number of larvae eaten per minute ± 1 standard deviation.

Experiment	Anemone Pedal diameter (mm)	N	Larval stage	Larval density (ml^{-1})	Feeding rate (min^{-1})
1	2-4	3	umbo	1	1.0 ± 0.8
2	2-4	4	umbo	4	2.4 ± 2.9
3	5-8	8	umbo	1	0.7 ± 0.6
4	5-8	7	umbo	4	2.8 ± 1.9
5	2-4	3	pediveliger	1	0.6 ± 0.7
6	2-4	4	pediveliger	4	1.1 ± 1.1
7	5-8	8	pediveliger	1	1.7 ± 1.2
8	5-8	7	pediveliger	4	4.9 ± 2.6

Digestion Times: Digestion time was considered to be the interval from the end of feeding to the first appearance in the experimental container of empty larval shell(s). A mean digestion time of about 4 h resulted. Results were generally consistent, with 8 out of 16 measurements falling in the 3.5 to 4.5 h range. The shortest interval of appearance of empty shells was 2.5 - 3.0 h; the longest was 5.0 - 5.5 h.

To check for digestion, the egested shells were examined. Of 163 pairs of hinged, intact shells examined, 133 (82%) were completely clear and empty. Of the remaining 30 pairs which retained some internal color or texture, none appeared to contain whole larvae.

Gut Content and Egestion Analysis: The gut of the 1 laboratory-fed sea anemone examined contained 50 pediveligers. Gut contents of 10 sea anemones freshly dredged from the Choptank River contained no bivalve larvae. Egested material from another 45 freshly dredged specimens collected at a later date yielded 1 complete pair of bivalve shells (comparable in size to those of oyster pediveligers) from each of 3 sea anemones.

Balanus improvisus

Ingestion Experiments: Results of these experiments are contained in Table 3. Compared with controls, larval

Table 3

Crassostrea virginica and *Balanus improvisus.* Effects of two sizes of barnacles on numbers of two stages of oyster larvae. Single barnacles left in presence of larvae in 200 ml of estuarine water for 18 h. Control bowls contained no barnacles. N = number of replications. Larval numbers at end of experiment are reported as mean ± 1 standard deviation.

Experiment	Barnacle opercular diameter (mm)	Larval stage	N	Larval numbers	
				Start	Finish
1	2-4	umbo	8	404	74 ± 58
2	5-8	umbo	8	404	51 ± 60
3	Control	umbo	8	404	130 ± 62
4	2-4	pediveliger	8	394	166 ±102
5	5-8	pediveliger	8	394	80 ± 76
6	Control	pediveliger	8	394	273 ± 39

Table 4

Diadumene leucolena and barnacles. Relative abundances on selected Chesapeake Bay oyster bars. Sample size per bar = 30 litres of oyster shell and associated material.

Oyster bar	Approximate location	*Diadumene leucolena*	Barnacles
Swan Point	38°08'N; 76°18'W	1	3583
Buoy Rock	39°00'; 76°13'	3	15943
Hood	38°56'; 76°14'	91	1289
Hollicutt Noose	38°51'; 76°21'	282	463
Cook Point	38°39'; 76°17'	377	78
Deep Neck	38°44'; 76°15'	250	782
Double Mills	38° 44'; 76°08'	52	133
Horn Point	38°36'; 76°08'	75	378
Green Marsh	38°35'; 76°04'	48	458
Norman	38°15'; 76°07'	235	547
Middleground	38°14'; 75°55'	495	1049
Georges	38°08'; 75°50'	244	64
Marumsco	37°57'; 75°44'	287	749
Sandy Pt. North	39°01'; 76°23'	345	4282
Saunders	38°53'; 76°29'	36	1599
Cornfield Harbor	38°03'; 76°20'	153	873

numbers decreased markedly in bowls containing barnacles. Homogeneity of variances was established as before and t-tests indicated that large barnacles had a statistically significant effect on both umbo larvae ($P < 0.05$) and pediveliger larvae ($P < 0.001$) compared with control values. Small barnacles significantly affected only pediveliger numbers ($P < 0.05$). However, upon comparing effects of barnacle size on survival of umbo or pediveliger larvae (experiment 1 vs. 2; 4 vs. 5), no statistical differences were noted ($P > 0.05$).

Egestion and Gut Content Analysis: Examination of gut content and feces of 25 freshly dredged *Balanus improvisus* revealed no evidence of bivalve larvae ingestion, nor were any bivalve shells noted in the bowls. For the 10 barnacles active in the presence of pediveligers in the laboratory for up to 12 h, we noted the following: more than 30 semidigested larvae in the gut of a large barnacle examined 1 h after initial exposure; no evidence of larvae in the gut of a small barnacle examined 1 h after initial exposure; no evidence of larvae in the feces and gut contents of the 7 barnacles examined 10 to 12 h after initial exposure; and 2 dead pediveligers inside the shell plates of a large barnacle examined 30 min after initial exposure to larvae.

Field Population Samples: Table 4 contains the results of our survey of 16 oyster bars conducted on July 19 and 20, and August 8, 1977. Numbers of sea anemones present varied from 1 to 495 per 30 L sample of dredged material. In general, barnacles predominated, averaging 92% of the animals counted. On some oyster bars (*e.g.*, Buoy Rock Bar), barnacles were extremely abundant, covering most of the available shell substrate. On other oyster bars (*e. g.* Cook Point, Georges) their numbers were relatively low.

DISCUSSION

Few reports exist regarding field densities of late-stage *Crassostrea virginica* larvae, and their gregarious nature in setting makes estimates ambiguous. Hidu & Haskin (1971) reported a 200 L sample taken in Delaware Bay to contain 4786 "eyed" larvae (0.024 mL^{-1}). Nelson (1924) reported densities in his samples of up to 250 mature larvae L^{-1} (0.25 mL^{-1}). While these reported densities are comparable to the lowest larval densities used in our ingestion experiments with *Diadumene leucolena,* it was shown in our experiments that sea anemones would almost completely eliminate larvae over the range of 0.1 to 6.4 larvae mL^{-1} (Table 1). Larvae are used as food as evidenced by egestion of empty shells. We expect that, as oyster pediveligers aggregate (whether passively or actively) over oyster shell preparatory to setting, sea anemones exact a toll, just as they did at the densities used in our experiments. *Balanus improvisus* (and presumably other species of barnacles in Chesapeake Bay) would appear to have a similar effect. Presence of semidigested larvae in one large barnacle exposed to pediveligers would indicate that the decline in larval numbers in the presence of barnacles (Table 3) is not just due to physical damage caused by contact with beating cirri but also involves feeding.

The few findings of oyster larvae in the guts of freshly dredged specimens of the invertebrate species cannot be construed as evidence that only limited ingestion of oyster larvae occurs in nature. We did not measure densities of oyster larvae in the water column over the oyster beds at the time of collection and our field collections were limited in number and over time. We expect that our laboratory observations demonstrating ingestion of oyster larvae by *Diadumene leucolena* and *Balanus improvisus* can be extrapolated to the field, although obviously these predators are exposed to a mixed food resource composed of more than just oyster larvae. There is no published evidence regarding selective feeding on oyster larvae in the presence of such a mixed resource. Nevertheless, when one considers the gauntlet of waving tentacles of sea anemones, beating cirri of barnacles, and filtering currents of adult oysters and an additional fouling species, the hooked mussel *Ischadium recurvum* (Rafinesque, 1820) (Reichardt, 1977) it becomes obvious that loss due to predation may be very high near or at the time of settlement by oyster larvae.

SUMMARY

Predation upon umbo and pediveliger larvae of *Crassostrea virginica* (oyster) by *Diadumene leucolena* (sea anemone) and *Balanus improvisus* (barnacle) was studied in the laboratory. Pre-feeding and feeding behavior of *D. leucolena* in the presence of oyster larvae was described. Few larvae survived in the presence of sea anemones. As larval density increased, sea anemones' feeding rates increased, with larger individuals generally feeding at a greater rate than smaller individuals. At 21° C to 22° C, larval shells were expelled about 4 h after ingestion of living larvae by sea anemones had occurred, on average. In the presence of *B. improvisus,* numbers of surviving larvae decreased significantly. Pediveliger larvae were found in the gut of a barnacle which had been kept in their presence for 1 h. Examination of guts of very limited numbers of freshly dredged individuals from the field provided evidence of bivalve larval shell in *D. leucolena,* but not in *B. improvisus.*

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